Bee Nutritional Demands

Subjects: Entomology

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Definition

For all bee species, the pollen quality determines the overall quality of the larval food, influences the development of individuals and shapes their populations. However, not all plants produce pollen that fully satisfies the nutritional requirements of bees. Lack of understanding of the nutritional requirements of wild bees may lead to unintended negative effects of conservation efforts. Ecological stoichiometry provides an approach to better understand the nutritional constraints on growing and developing organisms and their colonies and populations. It makes reference to elements that, if scarce in the environment, prevent the construction of biologically important organic molecules. The least understood aspect of the nutritional requirements of bees concerns stoichiometric balancing and the need for adequate ratios of nutritional elements in consumed food. This text provides theoretical foundation for the project aiming at determining the likely limitations imposed on wild bees by the lack of nutritionally balanced pollen.

The following hypotheses may be tested:

1. Pollen stoichiometry vary among plant species and populations but will differ more widely among species than within different populations of the same species.
2. The stoichiometry of bees will vary substantially among bee species and between sexes within a species, which suggests the existence of different nutritional demands. Therefore, it is expected that the stoichiometric mismatches experienced by bees will vary in a species-specific and sex-specific manner.
3. For a given bee species, specific pollen species allow the overcoming of stoichiometric mismatches and will balance the diet. Accordingly, it is expected expect that flora diversity and, thus, pollen diversity matches the stoichiometric niches of bees.

I predict that the occurrence of specific key host plant species that produce stoichiometrically desirable pollen allows bees to stoichiometrically balance their diets. The project may ask if and how floral diversity, particularly the accessibility of nutritionally desirable key species, may influence bee populations. The obtained data will allow the parameterization of a conceptual model of nutritional limitations (to be developed in the future), which will enable to predict how floral community influences wild bee populations via supply and demand of nutrients.

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1. Introduction

Having access to balanced food resources is crucial for the development, health and fitness of bees – which are essential pollinators that provide valuable ecosystem services [1] [2]. Alarmingly, wild bee populations are in decline due to the loss of floral diversity and a subsequent decrease in the nutritional quality of floral resources, such as pollen [1]. Pollen provides bees their primary source of nutrients and, therefore, is key for bee larval development, immunity, physiology, and adult reproduction [2]. Pollen quality, however, varies widely across space and time and among plant species, and bees must select pollen that meets their nutritional demands [2]. Similarly, the nutritional needs of different bee species and between larvae and adults vary extensively, which imply different nutritional constraints across species and along bee ontogeny [3] [4].

2. The Goal of the Project

Although floral diversity has been identified as an important factor for the fitness and population growth of pollinators, not all plants produce pollen that satisfies the nutritional requirements of bee larvae, and only some key pollen host plants provide balanced larval diets [3] [4]. **The goal of the project is to determine the nutritional limitations imposed on wild bees by the lack of nutritionally balanced pollen.** Therefore, one may **(i)** determine the nutritional value of the pollen produced by various plant species and **(ii)** estimate the nutritional needs of different species of wild bees. Finally, the combination of both research aims will enable to **(iii)** assess nutritional bottlenecks as determinants of the biodiversity of wild bee species.

3. Bee Nutritional Demands: Nutritional Ecology Approach

Nectar-feeding adult bees are energetically limited, whereas larvae are limited by the availability of body-building nutrients in their food, namely, pollen. Although floral diversity has been identified as an important factor that promotes the fitness and population growth of bees, it may act indirectly, i.e., via among-species differences in pollen nutritional quality [3] [4]. Bee larvae are highly vulnerable to changes in pollen due to their reliance on a fixed quantity and quality of food provided to them by adults. Therefore, even if adult bees have unlimited access to energy-rich nectar, bee populations and communities are shaped during the larval life stage by potential nutritional limitations that result from an unbalanced nutritional composition of pollen. Despite the importance of bee larvae-pollen quality interactions, the studies that consider bee nutrition have focused mostly on adults [2] [4]. Moreover, as studies of pollinators have mainly considered the domesticated bee, *Apis mellifera* L., the data related to wild species are limited, and a focus on the drivers of the current decline in the populations of wild native pollinators is needed [1] [5] [6].

The framework of ecological stoichiometry is a promising conceptual approach that helps to address an underlying mechanism of the nutritional ecology of bees, i.e., balancing the larval diet to enable larval growth, development and pupation into the adult body equipped with all the structures needed for maximal fitness [2]. The growth and development of every cell, tissue, organism and population is subject to the law of conservation of mass. Thus, organisms build their bodies by relying on thousands of chemical reactions, all of which must be chemically balanced. Therefore, an insufficient supply of certain elements in the food will likely prevent the production of tissues and physiologically important molecules that are constructed from this food either by the consumer itself or by its microbiota [2]. The demand for the resources used for growth and development is reflected in the stoichiometry of living organisms [7], i.e., the elemental phenotype of an organism [8]. Organismal stoichiometry is regulated homeostatically and is species-specific because it is a consequence of the particular structure, physiology and metabolism of different taxa [9] [10][11]. Consequently, a mismatch between the elemental phenotype of an organism's adult body and its larval food is expected to have negative fitness consequences [7] [12]. This phenomenon is called stoichiometric mismatch and is mathematically understood as much lower proportions of *Carbon:nutrient* in the consumer's body than in its food [11][13].

As living organisms require a diversity of nutrients to perform their biological functions, these functions can be limited by multiple nutrients simultaneously, where a shortfall of more than one chemical element can limit individual performance, population growth, and ecosystem function [14]. Ecological stoichiometry is a multivariate approach that uses multiple chemical elements as a metric [11]. Therefore, ecological stoichiometry can provide additional predictive power and complement traditional approaches to understand the role of nutrition in consumer-resource interactions [11]. However, after 30 years of the development of the framework of ecological stoichiometry and almost 20 years after the seminal book of Sterner and Elser [11] was published, the data on elemental phenotypes of a diversity of organisms are scarce and lag far behind the data on their genomes [14].

One way to understand the role of nutrient demands by consumers and supply by their resources is to use the approaches proposed by the biogeochemical niche and stoichiometric niche related to ecological stoichiometry [10] [15]. The stoichiometric niche is defined as the region of multivariate stoichiometric space (i.e., multiple elements) occupied by a group of individuals and/or species that helps to define their niche [10] [15]. As consumer species differ in their stoichiometries, to obtain stoichiometrically balanced food, they should prefer specific food sources that supply nutrients in the correct stoichiometric proportion. The current knowledge on pollen stoichiometry is based on only 14 studies on 85 pollen species that have been investigated over the last 80 years [3] [4]. From these 14 studies, only 5 contained data on hand-collected pollen (the majority of the studies considered honey bee-collected pollen pellets that contained pollen "contaminated" with nectar). Furthermore, the carbon (C) concentration, which is crucial for organisms to obtain energy and in stoichiometry, to quantify energy-nutrient imbalances, has never been reported for pollen apart from our own studies on polyfloral pollen loads collected by *O. bicornis* and *A. mellifera* [3][4][16]. The elemental phenotypes of only two bee species, namely, domesticated *A. mellifera* and wild *O. bicornis*, have been studied to date [3][4][16] and provided valuable new knowledge applicable to bee conservation efforts [3][4][16]. However, this is only a drop in the bucket compared with the amount of data that is needed to understand the nutritional ecology of bees.

Here, I propose to study the stoichiometry of chosen atoms in the biomass (body and cocoon) of of wild bees (i.e., their elemental phenotype; [8]), in two sexes, and in a diversity of pollen species. Accordingly, I propose to use the multidimensional stoichiometric approach to analyze which species of pollen are nutritionally limiting for specific bee species. The selection scheme should consider the data on the food sources preferred by particular bee species, the seasonality of bees and their potential food sources.

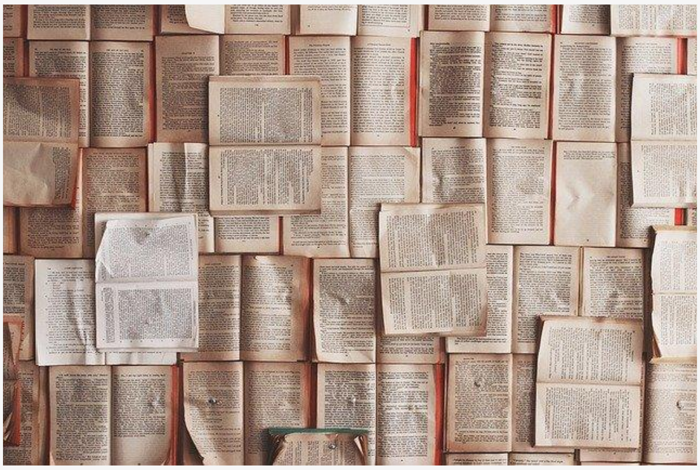
The following hypotheses might be tested:

1. Pollen stoichiometry vary among plant species and populations but will differ more widely among species than within different populations of the same species.

2. The stoichiometry of bees will vary substantially among bee species and between sexes within a species, which suggests the existence of different nutritional demands. Therefore, it is expected that the stoichiometric mismatches experienced by bees will vary in a species-specific and sex-specific manner.

3. For a given bee species, specific pollen species allow the overcoming of stoichiometric mismatches and will balance the diet. Accordingly, it is expected that flora diversity and, thus, pollen diversity matches the stoichiometric niches of bees.

3. Ecological Stoichiometry: Development, Current Knowledge, and A Brief Literature Overview



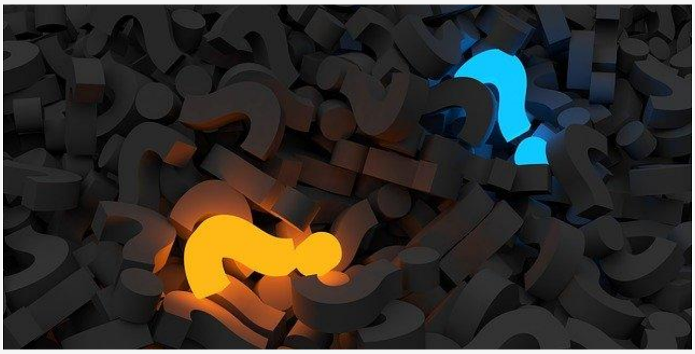
Consumers, especially herbivores, are faced with a high threshold of stoichiometric incompatibility between the chemical composition of their tissues and their food (Fig. 1). This observation has attracted the attention of ecologists and resulted in the development of a new research field, ecological stoichiometry [11]. Ecological stoichiometry raises questions concerning the strategies of crossing this threshold (the advantages and costs involved) and how these strategies affect the structure of communities and ecosystem functioning. The strategies for crossing stoichiometric thresholds are still poorly understood.

The atoms of chemical elements build the tissues and bodies of organisms in various proportions. This fact is crucial for ecological interactions and may shape the functioning of entire ecosystems [11]. The most fundamental feature of the elements, enabling their use in ecological stoichiometry, is that specific atoms cannot be transformed into different atoms by the organism. This feature distinguishes atoms from organic compounds. Within this context, ecological stoichiometry provides a common currency that links the ecology of organisms to life history trade-offs and evolutionary processes entrenched in the biogeochemical economy of life [7]. This currency is the ratio of atoms that compose the bodies of organisms and their food [11][17].

To date, ecological stoichiometry has provided data on elemental composition patterns in different trophic levels, with non-C element body contents tending to be the lowest in autotrophs, relatively low in herbivores and the highest in predators. Stoichiometric homeostasis has been shown be weaker in autotrophs and stronger in heterotrophs [11]. Ecological stoichiometry has also revealed stoichiometric mismatches at various trophic levels and has elucidated nutrient cycling in food webs [11][18][19]. However, these studies were conducted almost exclusively in aquatic ecosystems [20][21][22][23][24]. Recent studies have researched nutrient cycling in soil ecosystems and the relationship between stoichiometry and biodiversity [25][26][27][28][29][30], and considerable efforts have been made in the field of consumer-driven nutrient recycling theory (e.g., [31][32][33][34]). Nevertheless, much still needs to be done, since only C, N and P have been studied in this respect (e.g., [35]; see [22] for a review). The few papers on the stoichiometry beyond *C:N:P* almost exclusively concern freshwater systems [36][37][38][39], although limited data are available for marine ecosystems [40].

It was noted recently that it is easier to find in the scientific literature a population's genome than its elemental composition [14]. At the same time, the concept of stoichiometric niche was introduced and defined as the region of multivariate niche space occupied by a group of individuals where the axes represent their elemental content [10][15]. If a consumer is unable to find food that fits its stoichiometric niche, a limitation will be imposed on its growth and development that negatively influences its fitness, and the entire population may be negatively impacted in this way [7][12]. By using this concept within the framework of the current project, one might provide a useful tool based on ecological stoichiometry that allows us to predict the impact of changes in floral composition on populations of wild bees. To this end, one need to fill a knowledge gap concerning the elemental compositions of and stoichiometric relationships between wild bees and their potential foods.

4. The Framework of Ecological Stoichiometry: Overview



Limitations are imposed on organisms by the scarcity of organic substances in food, including specific amino acids [41]. However, it is practically impossible to incorporate into a single study the abundance of organic components that make food nutritionally balanced because of their wide diversity. Therefore, previous studies have focused on either (1) a specific group of organic substances (e.g., PLFAs or amino acids) or (2) the total concentrations of carbohydrates, proteins and lipids (reviews in [64–66]). Approach (1) provides only limited information on the nutritional ecology of bees, and method (2) overlooks the limiting effects of the scarcity of specific substances in food on bees that may exist even if the food contains a large amount of proteins, sugars or lipids. An alternative approach is to study the constraints imposed on organismal growth and development by unbalanced food within the framework of ecological stoichiometry [11]. This approach capitalizes on organisms that comprise identical building blocks – the atoms of chemical elements – although these building blocks create a remarkable diversity of molecules that have various functions [7][11][12]. During larval development, organisms assimilate all the building blocks needed to compose the adult body. The body is built of atoms in a taxonomically specific proportion known as the organismal stoichiometry [7]. The demand for resources gathered during larval growth is reflected in the organismal stoichiometry of the adult body, and a stoichiometric mismatch may occur between the atomic composition of the body and the larval food [11]. Toxic effects may, in fact, be caused by such a stoichiometric mismatch rather than truly toxic substances [42]. Adult food, which is rich in energy, has different characteristics than larval food, which is rich in body-building matter. Wild bees may have an almost infinite access to energy-rich food (nectar) that meets the nutritional needs of the energetically limited adults. However, the quantity of food for bee larvae (pollen) cannot be substituted for its quality, and a poor nutritional balance in the pollen consumed may limit the growth and development of individuals, which negatively influences their populations [11][41].

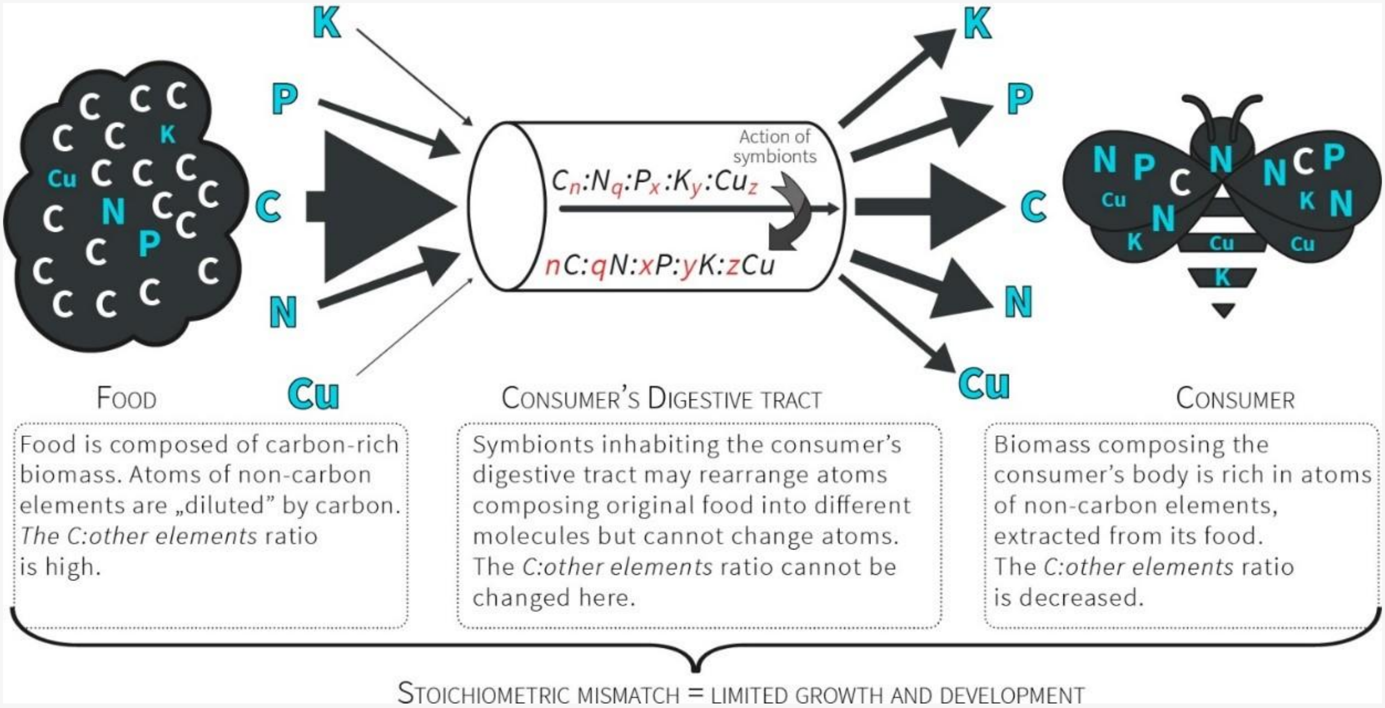
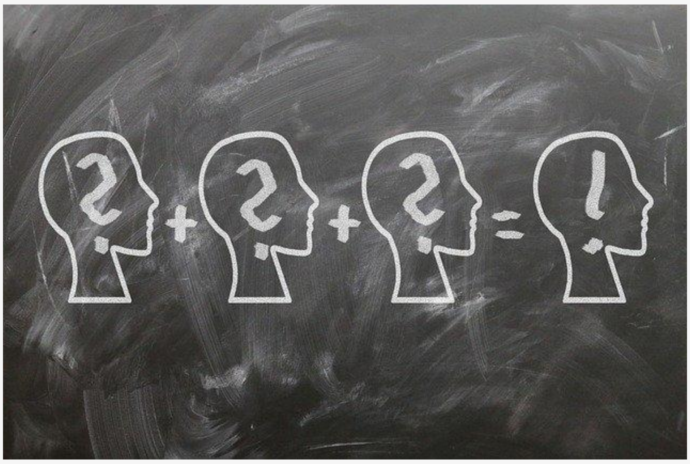


Fig.1. Consumers ingest a prepackaged ratio of atoms. For herbivores, their food contains more C relative to other atoms; therefore, they must manage a diet that presents a stoichiometric mismatch through excess C that is further exacerbated by the unbalanced relationships between non-C elements (due to the exceptional scarcity of some of them).

5. Trophic Stoichiometric Ratio (*TSR*) - the Measure of Stoichiometric Mismatch for Bees that Feed on Various Pollen Species



The fundamental index in ecological stoichiometry is the threshold elemental ratio (*TER;* [11][13][23]). This index allows for the calculation of the limiting effect imposed on an organism by stoichiometric mismatches. The threshold elemental ratio is the lowest atomic ratio of *C:other element* in food at which the consumer's development is not limited by the scarcity of C (i.e., energy) but is limited by the scarcity of the non-C element in the food. The basis for calculating the *TER* represents the consumer's requirement for any non-C element during growth and development. This requirement is represented by utilizing the consumer's consumption rates, assimilation rates and respiration rates of C and the non-C element. Therefore, the *TER* considers both (1) the energy budget, which is measured as the C balance, and (2) the budget of any non-C element.

The *TER* is understood as follows:

$TER_x = (GGE_x / GGE_c)*(C:X)_{i+1}$

where GGE_x is the gross growth efficiency of element *x*, GGE_C is the gross growth efficiency of carbon, *i* is the trophic level, *C* is the concentration of carbon, and *X* is the concentration of element *x*.

If:

$(C:X) \geq TER_x$

then element *x* may become a limiting factor for growth at trophic level *i+1*.

The *TER* for any *C:X* ratio, where *X* is any element other than C, may be calculated as follows:

$TER_x = \{A_x / [(I_c A_c - R_c) / I_c]\}*(C:X)_{i+1}$

where A_X and A_C are the assimilation rates for elements C and X, respectively, I_C is the C ingestion rate, R_C is the C respiration rate, and $(C:X)_{i+1}$ is the atomic ratio of *C:X* in the consumer's body.

However, in the case of herbivorous invertebrates, utilizing this index for certain elements is technically impossible. The gross growth efficiencies should be experimentally measured by using laboratory feeding trials in growing animals. Such data are extremely scarce, particularly for elements other than N and P. In practical terms, the *TER* index for invertebrates can only be estimated with arbitrary assumptions [35][43][43]. To allow for the identification of multiple elements that co-limit the development of an organism and facilitate comparisons between various taxa, habitats, food and life histories, the trophic stoichiometric ratio (*TSR*) was developed. The *TSR* is a simplified version of the *TER* that solely utilizes the data on the elemental composition of the organism and its food, and feeding experiments are not required [43][44]. The *TSR* is based on the following:

$(C:X)_i / (C:X)_{i+1} \geq GGE_x / GGE_c$

The minimum balanced GGE_x / GGE_C ratio can be estimated as 1/0.25 = 4, assuming that 75% of the consumed carbon is released as CO_2 while the other consumed elements are incorporated with a 100% efficiency. Accordingly, it is conservatively assumed that for $(C:X)_i / (C:X)_{i+1} \geq 4.0$, element *x* may impose a constraint on growth [43][44]. Therefore, the *TSR* is calculated as follows[43][44]:

$TSR_x = (C:X)_{food} / (C:X)_{consumer}$

where *C* is the concentration of carbon and *X* is the concentration of element *x*. Therefore, a $\boldsymbol{TSR_x \geq 4}$ indicates a limitation imposed on the growth and development of an organism that feeds on the given food caused by the scarcity of element *x* in the food. When the *TSR* value is higher, the limiting effect is more severe.

Various elements may be differentially acquired, assimilated, reused, and excreted. The *TSR* index compares the elemental composition of an animal's body and the food eaten (not the food assimilated). The absorbed matter has a different elemental composition than the ingested matter, but to absorb this and to void the indigestible surplus, the physiological effort must be proportional to the difference between the food eaten and the food assimilated to which the stoichiometric mismatch represented by the *TSR* index is proportional. Because the *TSR* index assumes that noncarbon elements are assimilated from food at a maximum rate (100%), the actual mismatches in natural situations can only be greater than the estimated *TSR* values. Therefore, the *TSR* index serves as a conservative but convenient tool that facilitates not only the detection of elements that co-limit development but also comparisons of the severity of the limitations imposed by various foods on different consumers.

The *TSR* index is used in the present project to study stoichiometric mismatches for bees that feed on various pollen species. Thus, it is possible to detect plant species that are stoichiometrically adequate/inadequate for specific bee species and that therefore positively/negatively influence bee communities and populations.

6. Expected Impact of the Research Project on the Development of Science

The link between floral diversity/composition and bee performance is unclear. We do not yet understand the differential contribution of various nutrients to bees' growth and development. Are there species-specific key nutrients or nutrient ratios linked to development? Are such key nutrients associated with specific key plant species? Accordingly, can increased bee fitness (which is typically found in, for example, more diverse environments) be better predicted by optimal ratios of nutrients? Answering these questions will shed light on the mechanisms that underlie the known positive correlation between floral biodiversity and bee prosperity. However, the project has wider significance, as ecological stoichiometry aims to explain the adaptive strategies that compensate for stoichiometric mismatches, the costs and benefits involved, and how these strategies affect the structure of biotic communities and ecosystem function. The strategies used to overcome these mismatches by various herbivorous taxa remain poorly understood, especially considering terrestrial ecosystems. The proposed research will help to address this gap.

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Keywords

bee;wild bee;bees;insect;entomology;ecology;physiology;ecophysiology;nutrition;nutritional ecology;pollen;project;idea;conservation;ecological stoichiometry;stoichiometry;food;pollinator;decline